EPIDERMAL STUDIES IN THE INTERPRETATION OF *LEPIDODENDRON* SPECIES

by B. A. THOMAS

ABSTRACT. Thirteen species of *Lepidodendron* are described including two new species *L. arberi* and *L. barnsleyense*. Details of the epidermis are given and its use in species distinction and classification is considered. Cuticle information about secondary growth is also discussed.

LEPIDODENDRON is an arborescent lycopod stem genus characterized by the persistent basal parts of leaves (leaf cushions) from which the apical parts have often been shed. The compression species, like those of most other fossil lycopod genera, have been described and classified on external gross morphology. Text-fig. 1 illustrates the cushion features most useful in classification. However, the actual naming of a specimen, especially a badly preserved one, is still sometimes difficult because many species appear similar in one or more details. The lycopod cuticle has been largely ignored as a possible descriptive character even though epidermal characters have been shown to be of great importance in other plant groups. The value of the lycopod cuticle has already been discussed (Thomas 1966) but detailed descriptions of *Lepidodendron* cuticles are given here showing how a study of them can assist in the definition and distinction of species.

Whenever possible the type specimen was examined together with several other specimens to detect any variation within the species. However, specimens from which cuticle could be prepared were often difficult to find. Some type specimens and many others are preserved as impressions and some of those which are compressions have finely cracked carbon which does not yield cuticle. Examination of the cushion surface is sometimes useful when the cuticle cannot be prepared as the epidermal cells and stomata are often visible.

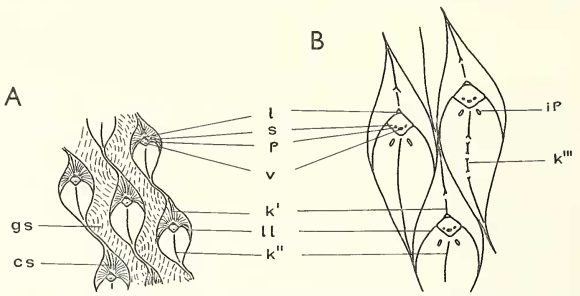
Cuticle was prepared by macerating portions of the carbonized compression in Schulze solution followed by clearing in dilute ammonia solution. The cuticles were mounted unstained in glycerine jelly and examined by normal transmitted light supplemented in a few instances by phase contrast illumination. The cuticle preparations have been deposited with their respective specimens.

The specimens were borrowed from or deposited in: the British Museum of Natural History, London (BMNH); the Kidston collection of the Geological Survey and Museum, London (K); the general collection of the Geological Survey and Museum, London (GSM); the Geological Survey, Leeds (GSL); the Geological Survey, Edinburgh (GSE); the Sedgwick Museum, Cambridge (SM); the Warwickshire County Museum, Warwick (WM); the Leicester City Museum (LM); the Royal Scottish Museum, Edinburgh (RSM), and the Czechoslovakian National Museum, Prague (CNM).

Acknowledgements. I would like to thank Professor T. M. Harris, F.R.S. for his help and guidance throughout much of this study; the directors and staff of the museums for allowing me to borrow and

[Palaeontology, Vol. 13, Part 1, 1970, pp. 145–73, pls. 29–34.]

make preparations from specimens in their collections; the National Coal Board and Open Cast Executive for permitting my access to their workings; the site officials who helped me to collect specimens; the Coal Board Scientific Staff for help in certain correlation problems; the University of Reading Research Board from whom I was in receipt of a research studentship, and the University of Newcastle upon Tyne and the Royal Society of London for travel grants. The work was completed during the tenure of the Lord Adams Research Fellowship at the University of Newcastle upon Tyne.



TEXT-FIG. 1. Drawings of diagrammatic leaf cushions to illustrate their main features. A, Leaf cushions continuous with other cushions above and below but separated from those on either side by wrinkled areas of bark. B, Closely packed leaf cushions not continuous with other cushions above and below. cs—cushion striations; gs—inter cushion striations; ip—infrafoliar parichnos; k′—cushion keel above the leaf scar; k″—cushion keel below the leaf scar; k‴—cushion keel broken by transverse notches; l—ligule pit aperture; ll—lateral line running from leaf scar to cushion edge; p—foliar parichnos; s—leaf scar; v—vascular print.

SYSTEMATIC DESCRIPTIONS

Lepidodendron aculeatum Sternberg

Plate 29; Plate 30, figs. 1, 5; Plate 31, figs. 1–3; text-figs. 2, 3

1820 *Lepidodendron obovatum* Sternberg, pp. 20, 23, pl. 6, fig. 1; pl. 8, figs. 1A, *a*, *b*.
1820 *Lepidodendron aculeatum* Sternberg, pp. 20, 23, pl. 6, fig. 2; pl. 8, figs. 1B, *a*, *b*.
1820 *Lepidodendron crenatum* Sternberg, pp. 20, 23, pl. 8, fig. 2B.
1821 *Lepidodendron aculeatum* Sternberg, pl. 14, figs. 1–4.
1838 *Sagenaria aculeata* Presl in Sternberg, p. 177, pl. 68, fig. 3.
1838 *Sagenaria rugosa* Presl in Sternberg, p. 177, pl. 68, fig. 4.
1838 *Sagenaria caudata* Presl in Sternberg, p. 178, pl. 68, fig. 7.
1877 *Lepidodendron aculeatum* Sternberg; Fairchild pars, p. 77, pl. 5, figs. 1–4; pl. 6, figs. 1–5; pl. 7, figs. 1–4; pl. 8, figs. 1, 2.
1886 *Lepidodendron aculeatum* Sternberg; Zeiller, p. 435, pl. 65, figs. 1–7.

EXPLANATION OF PLATE 29

Lepidodendron aculeatum Sternberg. Fig. 1, CNM ČGH 365; Type specimen of Sternberg 1820, pl. 6, fig. 2. Fig. 2, CNM ČGH 658 (= *Lepidodendron obovatum* Sternberg 1820, pl. 6, fig. 1). Fig. 3, CNM ČGH 805 (= *Sagenaria rugosum* Presl *in* Sternberg 1838, pl. 68, fig. 4). Fig. 4, CNM ČGH 792 (= *Sagenaria caudata* Presl *in* Sternberg 1838, pl. 68, fig. 7).
All at × 1.

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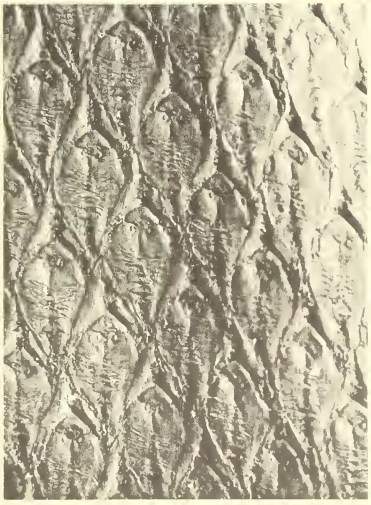

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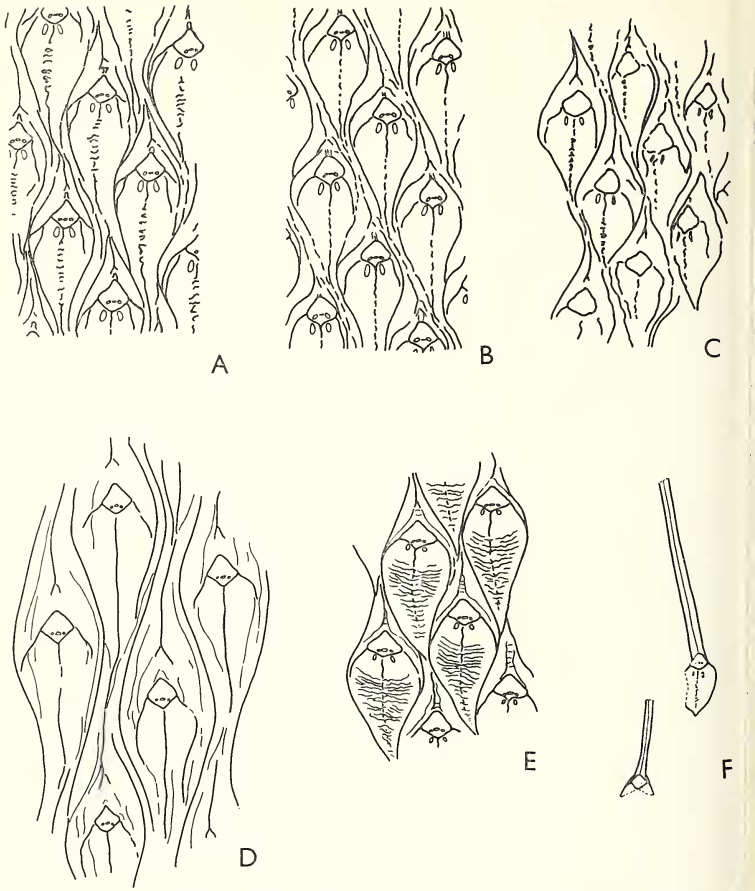
THOMAS, *Lepidodendron*

1899 *Lepidodendron aculeatum* Sternberg; Potonié, p. 220, text-fig. 211.
1904 *Lepidodendron aculeatum* Sternberg; Zalessky, p. 81, pl. 1, figs. 1–6; pl. 2, fig. 2.
1947 *Lepidodendron aculeatum* Sternberg; Němejc pars, p. 49.
1959 *Lepidodendron aculeatum* Sternberg; Remy, p. 98, text-figs. 76, *a*, *b*.
1964 *Lepidodendron aculeatum* Sternberg; Crookall, p. 233, pl. 60, fig. 6; text-fig. 77*a*.

Material. Type specimen CNM ČGH 365 from the Upper Carboniferous of Radnice, Bohemia; CNM ČGH 658 (*L. obovatum* Sternberg 1820, pl. 6, fig. 2.) from Radnice; CNM ČGH 660 (*L. crenatum* Sternberg 1820, pl. 8, fig. 2в) from Radnice; CNM ČGH 792 (*Sagenaria caudata* Presl in Sternberg 1838, pl. 68, fig. 4) from the Upper Carboniferous, Waldenburg, Silesia; CNM 23072 from the Mydlak horizon of Kladno; WM G. 541, from the Westphalian coal measures of Tamworth, Staffordshire; BMNH 1049, from the coal measures of Waldenburg, Silesia; BMNH 46685, from the Westphalian coal measures of Ebbw Vale, Monmouthshire; BMNH 41308, from the Mushett Blackband Ironstone, No. 6 pit, Monkland, near Airdrie, Scotland; Westphalian B.

All the specimens possess the same general cushion characters. The cushions have inflexed, pointed upper and lower angles and rounded lateral angles. The leaf scars are diamond-shaped, about as long as broad, and are situated about one-third the distance down the leaf cushions. There are three foliar prints, though sometimes only one can be seen, and two infrafoliar parichnos. The ligule pit aperture is adjacent to the upper angle of the leaf scar and not a short distance above as it is often figured. There are prominent keels above and below the scar and lateral lines curve from the lateral angles of the leaf scars to the edges of the leaf cushion. The keels are normally smooth and continuous above the leaf scar but are divided by notches below the scar. The leaf cushion surface is smooth. BMNH 1049 and BMNH 41308 have very plain infrafoliar parichnos but although repeated attempts have been made to prepare cuticle from them none was obtained and I am convinced there never was any. Most specimens of this species show the leaf cushions close together but some, e.g. BMNH 1049, have them separated by wrinkled areas of bark. These wrinkled areas have been thought to be of diagnostic value, for example Lesquereux (1879/80) used their presence as the main character for his *Lepidodendron modulatum*. It is now commonly accepted that they are the result of lateral expansion of the bark produced during the secondary growth of the stem (for further discussion see Eggert 1961 and Chaloner 1967). The wrinkles have been described as fissures or cracks in the bark by Fairchild (1877). However as cuticle was prepared from the whole area in BMNH 1049 it is more likely that they were formed by a secondary production of epidermis interspersed between the original epidermis of the furrow. This formation of extra epidermis seems to have been accompanied by a stretching out and shallowing of the intercushion groove. Preparation of cuticle from the intercushion areas of BMNH 1049 shows that the furrows possess roughly isodiametric epidermal cells and stomata while the interconnected ridges have epidermal cells elongate across the ridges and no stomata. The cuticle without stomata probably represents the secondary produced epidermal areas especially as those specimens with close cushions have stomata within their intercushion grooves.

CNM 23072 has many isolated leaf cushions with leaves still attached. The leaves are at least 11 cm. long but all are incomplete and only the slightest narrowing can be seen. Even though the leaves are attached three foliar prints are visible showing that their presence is not necessarily indicative of prior leaf fall. A central median vein can be clearly seen on all leaves and on a few an additional line is present on either side of the median, which probably represents a stomatal groove. Not all the leaves show stomatal



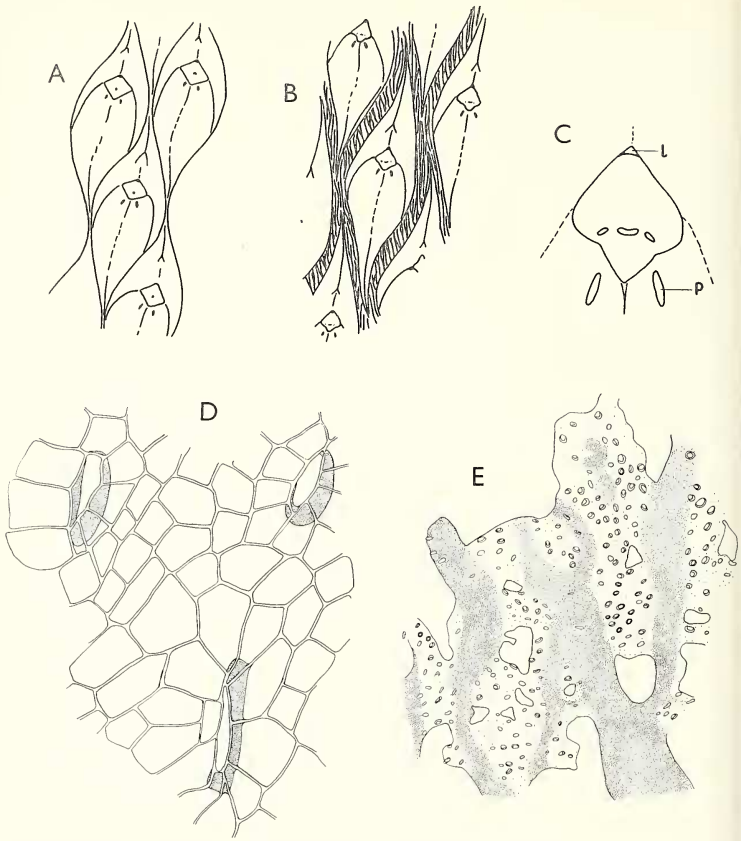
TEXT-FIG. 2. *Lepidodendron aculeatum* Sternberg. A, CNM ČGH 365; Type specimen of Sternberg 1820, pl. 6, fig. 2. B, CNM ČGH 658 (= *L. obovatum* Sternberg 1820, pl. 6, fig. 1). C, CNM ČGH 660) (= *Lepidodendron crenatum* Sternberg 1820, pl. 8, fig. 2B). D, CNM ČGH 792 (= *Sagenaria caudata* Presl *in* Sternberg 1838, pl. 68, fig. 7). E, CNM ČGH 805 (= *Sagenaria rugosa* Presl *in* Sternberg 1838, pl. 68, fig. 4). F, CNM 23072; showing leaves still attached to the leaf cushions. All illustrations at ×2.

grooves as their visibility is of course dependent on the orientation of the leaves. Such long leaves with stomatal grooves, if found detached, would undoubtedly be determined as *Cyperites bicarinatus* Lindley and Hutton, confirming the reports of the possession of such leaves by *Lepidodendron aculeatum* given by Crookall (1966, p. 535) and Chaloner (1967, p. 673). Unfortunately no cuticle could be prepared from these attached leaves and no epidermal detail could be discerned by direct observation.

Cuticle description. The epidermal cells from all over the cushion surface are roughly isodiametric and 15–20 μ across, except near the cushion edges where they are mostly 30 $\mu \times 15$ μ and elongated towards the cushion centre. However, in BMNH 46685, where the keel is more prominent and divided by many transverse notches, the epidermal cells near the keel are elongated towards the keel and are typically 30 $\mu \times 18$ μ in size. The anticlinal walls are straight, smooth and about 2 μ thick. The perclinal walls are flat and smooth. The stomata are about 200–250 per mm.^{2}, randomly distributed and orientated, but in BMNH 46685 they are absent on the keel lumps and very sparse in the keel notches. Stomatal average size is about 40 $\mu \times 18$ μ and the guard cells are sunken in pits 12–15 μ deep. There are about nine subsidiary cells to each stoma, unmodified except for sometimes being slightly elongated away from the stomata. In the wrinkled intercushion areas there are interconnecting strands of dark cuticle separating patches of lighter brown cuticle. The dark cuticle has epidermal cells 30 $\mu \times 15$ μ elongated at right angles to the strands, but the lighter cuticle has isodiametric cells about 20–30 μ broad. Stomata are about 340 per mm.^{2} in the lighter cuticle but are very few and restricted to the edges of the dark cuticle. The stomata are 25–30 $\mu \times 10$ μ in size and the guard cells are sunken in pits 10–15 μ deep. The ligule pit cuticle is about 0·45 mm. broad and at least 2 mm. long. The lining cells are rectangular, 45 $\mu \times 15$ μ, and elongated along the pit.

Comparison. Specimens similar to Sternberg's figures of *L. obovatum* and *L. aculeatum* have been commonly found and described. However, the two species have not always been interpreted in the same way and indeed many authors have changed their views from one paper to another. Some authors have accepted only part of Sternberg's descriptions and figures, others have placed some of his other species in synonymy with these two species, while a few have united the two. These varying opinions seem to have arisen as a result of differing ideas about the value of Sternberg's figures and the emphasis put on different cushion characters.

A study of Sternberg's specimens has shown that his interpretation needs to be modified. I agree basically with Němejc (1947) in his reinterpretation but differ slightly in the synonymy lists quoted. The illustration of the type specimen of *L. obovatum* (Sternberg 1820, pl. 6, fig. 1) fails to show accurately the upper angle of the cushions and the keel ornamentations. The upper angle is pointed as is the lower angle and not rounded as the illustration suggests and the keel below the leaf scar is divided by transverse notches. When *L. obovatum* is interpreted in this manner, there is no difference between it and the subsequently described *L. aculeatum*. Specimens of this form have been, and indeed still are, commonly named *L. aculeatum*. Fischer (1904) united the two species under *L. obovatum* but included in his synonymy other forms which are quite different, e.g. the *L. obovatum* of Presl. This broad interpretation of *L. obovatum* is quite unacceptable and I believe the best solution is to regard *L. obovatum* as a confused name



TEXT-FIG. 3. *Lepidodendron aculeatum* Sternberg. A, B, Leaf cushions before and after secondary expansion of the stem, ×1. C, Leaf scar with ligule pit (l) and infrafoliar parichnos (p). D, Leaf cushion cuticle, ×400. E, Cuticle from expanded bark between the leaf cushions showing dark cuticle with none or very few stomata and light-coloured cuticle with many stomata, ×20. A, C, E, from WM G541; B, D, from BMNH 1049.

reduced to a synonym of the more commonly used *L. aculeatum*. Presl, in Sternberg (1838), described a specimen (pl. 68, fig. 6) as *L. obovatum*. However this is not *L. obovatum* Sternberg, i.e. *L. aculeatum* Sternberg. The cushions are broader and have no drawn out inflexed upper and lower angles. The leaf scars are broader than long while in *L. aculeatum* they are about as long as broad. The cushion surface above the leaf scar is finely striated while in *L. aculeatum* it is smooth. Finally the infrafoliar parichnos are not so well defined as in *L. aculeatum*. Nevertheless, many workers have described specimens as *L. obovatum* because they resembled Presl's specimen named as *L. obovatum*. Now in an attempt to discover the name that should be applied to Presl's specimen, I found that *L. mannabachense* Presl in Sternberg (1838, pl. 68, fig. 2) is identical to the now commonly accepted form of *L. obovatum*. A description of this species is given later.

Sagenaria caudata Presl, *S. rugosa* Presl, and *Lepidodendron crenatum* Sternberg should all be referred to *L. aculeatum* Sternberg. The type specimen of *S. caudata* is an almost flat compression and, although the original illustration is not very informative, clearly shows the typical features of *L. aculeatum*. *S. rugosa* is best regarded as *L. aculeatum* although several authors have included it in *L. obovatum* sensu Presl. The type specimen differs from *L. aculeatum* only in having leaf scars which are slightly broader than long; this alone seems insufficient for species distinction. In contrast, Presl's (1838, pl. 68, fig. 5) specimen of *S. crenatum*, CNM ČGH 322, has leaf scars quite unlike those of *L. aculeatum* and is not this species. The leaf scars are as broad as the cushions and are situated just above their centres.

Lepidodendron serpentigerum Koenig

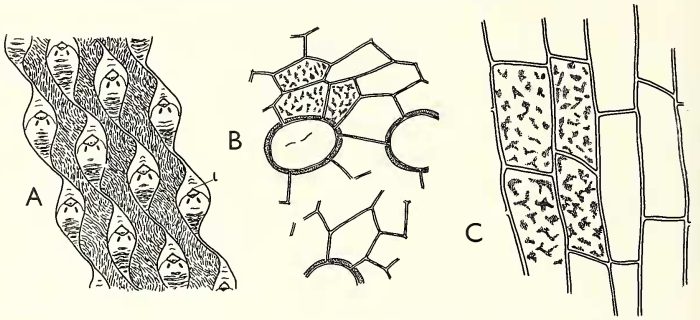
Plate 31, fig. 4; Plate 34, fig. 6; text-fig. 4

1825 *Lepidodendron serpentigerum* Koenig, pl. 16, fig. 195.
1902 *Lepidodendron serpentigerum* Koenig; Kidston, pp. 345, 371, pl. 51, fig. 2.
1906 *Lepidodendron serpentigerum* Koenig; Fischer pars, No. 75, figs. 1, 2.
1927 *Lepidodendron serpentigerum* Koenig; Hirmer, pp. 200, 204, text-fig. 237.
1964 *Lepidodendron serpentigerum* Koenig; Crookall, p. 260, pl. 61, fig. 5, text-fig. 83.

Material. Neotype, BMNH 39020 from the Westphalian Coal Measures, Newcastle upon Tyne (Crookall 1964, text-fig. 83); K 2498 from above the Stranger Coal, Granger Colliery, Kilmarnock, Ayrshire (Kidston 1902, pl. 51, fig. 2; Crookall 1964, pl. 61, fig. 5), Westphalian B; SM 3148 from the Transition Coal Measures of the Bishopsbourne Boring, Barham Down, 4 miles south-east of Canterbury, Kent.

The three specimens are very similar in having their leaf cushions connected above and below by inflexed cushion extensions and separated on either side by wrinkled areas of bark. The leaf scars are two-thirds the distance up the cushions and possess three conspicuous foliar prints. The ligule pit aperture is adjacent to the upper angle of the leaf scar and there are two plainly visible infra-foliar parichnos. The keels are more prominent below the leaf scars and are divided by many transverse grooves. No cuticle could be prepared from the neotype and only small fragments from the other two. K 2498 gave good cuticle from the wrinkled intercushion areas but poor cuticle from the leaf cushions and SM 3148 gave reasonable cuticle from the leaf cushions but none from the wrinkled areas.

Cuticle description. The cuticle is similar over the whole leaf cushion surface. The epidermal cells are about 35 μ across, roughly isodiametric or slightly elongated. The anticlinal walls are straight, smooth and about 2 μ thick. The periclinal walls are flat and granular. The stomata are about 50 $\mu \times 30$ μ in size and the guard cells are sunken



TEXT-FIG. 4. *Lepidodendron serpentigerum* Koenig. A, Leaf cushions from K2498, $\times 1$; Ligule pit (1). B, Cushion cuticle from SM 3148, $\times 400$. C, Cuticle from intercushion areas of K2498, slide PF 3144. The granular surface of the cuticle seen under phase contrast is represented in only a few cells of B and C.

in pits 4 μ deep. The cuticle from the inter-cushion areas is thicker than that from the cushion surface and has roughly rectangular cells, 60 $\mu \times 20$ μ, elongated parallel to the intercushion striations. The anticlinal walls are straight, smooth, and 3 μ thick and the periclinal walls are flat and granular. There are no stomata in the intercushion areas.

Comparison. Lepidodendron zeilleri Zalessky (1904, p. 91, pl. 4; fig. 1, 1*a*) is almost certainly a synonym of *L. serpentigerum.* The only difference between the two type specimen figures is that *L. zerilleri* has more rounded upper angles to the leaf scars which is not a distinctive enough character for species separation.

Němejc (1947, p. 62) believed that *L. serpentigerum* was similar to *L. obovatum* Presl, non Sternberg (= *L. mannabachense* Presl) and *L. aculeatum* Sternberg and that it was probably only a growth form of the latter. However the cushions of *L. serpentigerum* are more S-shaped than both these species and possess different cushion and epidermal

EXPLANATION OF PLATE 30

Fig. 1, *Lepidodendron aculeatum* Sternberg, CNM ČGH 660 (= *Lepidodendron crenatum* Sternberg 1820, pl. 8, fig. 2B).

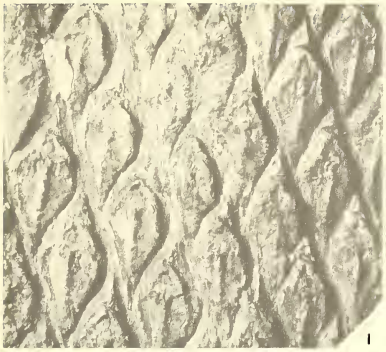
Fig. 2, *Lepidodendron veltheimii* Sternberg, CNM ČGH 330; figured by Presl *in* Sternberg 1838, pl. 68, fig. 14.

Fig. 3, *Lepidodendron mannabachense* Presl, CNM ČGH 355 (= *Sagenaria obovatum* Presl *in* Sternberg 1838, pl. 68, fig. 2).

Fig. 4, *Lepidodendron mannabachense* Presl (type specimen), CNM ČGH 329; figured by Presl *in* Sternberg 1838, pl. 68, fig. 2.

Fig. 5, *Lepidodendron aculeatum* Sternberg, with leaves attached to leaf cushions, CNM 23072.

All at $\times 1$.



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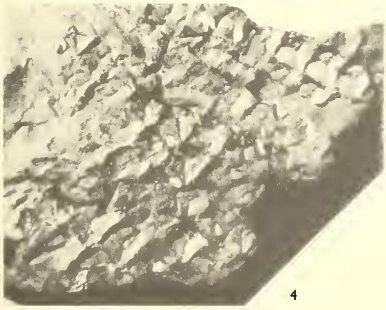

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details. *L. mannabachense*, unlike *L. serpentigerum*, has striations on its leaf cushions and has dissimilar epidermal arrangements above and below the leaf scars. *L. aculeatum* Sternberg has broader leaf scars, more prominent keels, smaller epidermal cells, and deeper stomatal pits than *L. serpentigerum*. The form of *L. aculeatum* with separated leaf cushions also differs in the cuticle details obtained from the intercushion areas. In *L. aculeatum* there are strips of epidermis with stomata alternating with strips with no stomata whereas in *L. serpentigerum* the epidermis is all similar and possesses no stomata.

Lepidodendron veltheimii Sternberg

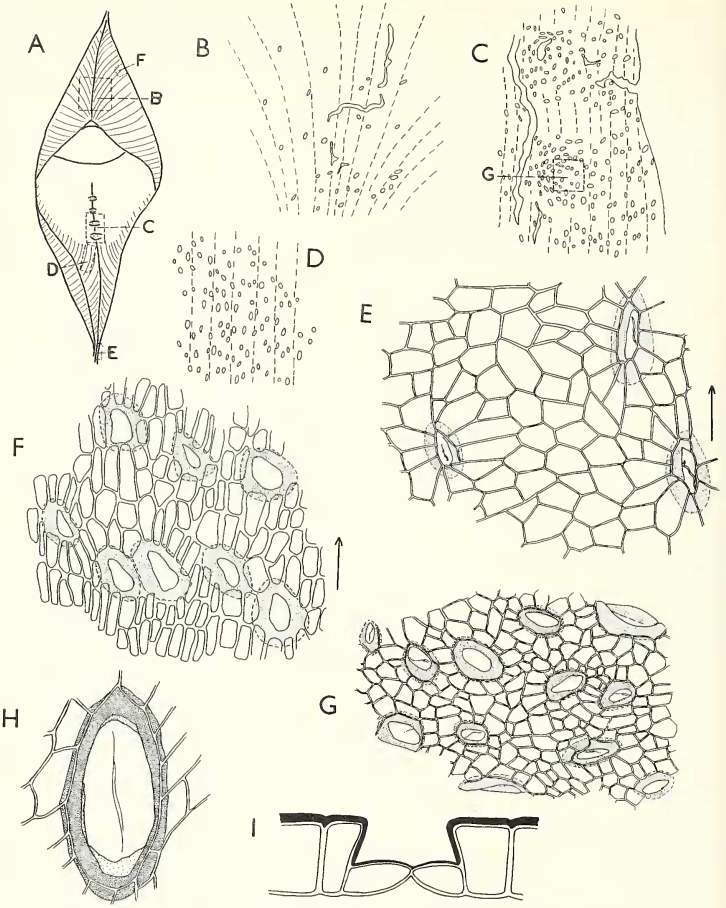
Plate 30, fig. 2; Plate 33, figs. 4–6; text-fig. 5

1825 *Lepidodendron Veltheimii* Sternberg, p. 43, pl. 52, fig. 3.
1838 *Lepidodendron Veltheimianum* Presl in Sternberg, p. 180, pl. 68, fig. 14.
1899 *Lepidodendron Veltheimianum* Sternberg; Hoffman and Ryba, p. 78, pl. 15, figs. 7, 8.
1926 *Lepidodendron Veltheimianum* Sternberg; Kidston, p. 147, pl. 13, fig. 2.
1964 *Lepidodendron veltheimi* Sternberg; Crookall, p. 298, pl. 64, figs. 3–5; pl. 70, fig. 8; pl. 71, figs. 1, 2; text-figs. 77*c*, 96.

Material. CNM ČGH 330 from the Lower Carboniferous of Magdeburg (probably the specimen figured by Presl 1838, although it also bears a label referring it to Sternberg 1825); K 2411 from immediately beneath the Orchard Limestone, New Brawden Quarry, Giffnock, Renfrewshire, Upper Limestone Group of the Carboniferous Limestone Series, Lower Namurian.

CNM ČGH 330 is an impression with no carbon remaining and no visible epidermal details, so all the information about the epidermis was obtained from K 2411. This is a fairly thick compression on a slab of black shale. The leaf cushions are in low-angle spirals of about 25° to the horizontal and are continuous with the cushions above and below by inflexed apical and basal angles. The leaf scar is prominent but only one foliar print can be seen and no infrafoliar parichnos are visible. The ligule pit aperture is adjacent to the upper angle of the leaf scar. The keel is prominent, but interrupted in the upper part below the leaf scar. The carbon of the compression is not cracked as in most specimens and large pieces of well-preserved cuticle could be prepared from it.

Cuticle description. The cuticle from the grooves between the cushions is about 3–4 μ thick. The epidermal cells are isodiametric, 20 μ across, or elongated up to 40 μ. The anticlinal walls are straight, smooth, and 2–3 μ thick. The periclinal walls are flat and smooth. No stomata were visible in the grooves but some are present near the edges of the cushion. The leaf cushion cuticle is 2 μ thick. The epidermal cells are isodiametric, 15–20 μ, or elongated up to 40 μ. The long axes of the cells tend to form curves running from the cushion edge towards the keel and then parallel to it. The cells do not form well-developed rows, but sometimes are in small groups appearing to have been formed by the transverse division of one cell. The anticlinal walls are straight, smooth, and 2–4 μ thick. The periclinal walls are flat and smooth. Stomata are about 60 per mm^2. on the cushion below the leaf scar but slightly less above it. They are randomly distributed over most of the cushion, but are arranged concentrically around the lumps which make up the keel just below the leaf scar. The guard cells are sunken in overhanging, thick-walled stomatal pits, 15 μ deep. The stomatal apertures are usually oval, but occasionally rounded, and of average size 60 $\mu \times 40$ μ. The subsidiary cells are usually 8–12 in number



TEXT-FIG. 5. *Lepidodendron veltheimii* Sternberg. K2411. A, Leaf cushions, ×3. The lines on the cushion indicate the direction and area covered by surface striations, but they do not represent individual striations. B, C, D, Areas of cushion surface showing direction of striations and distribution of stomata, ×20. Slide nos.: B—PF 2699; C. D—PF 2700. E, Cuticle from groove between cushions, arrows directed parallel to the groove, slide PF 2701, ×200. F, Cuticle from edge of cushion, arrow directed away from groove, slide PF 2698, ×200. G, Cuticle from cushion surface, slide PF 2700, ×200. H, Stoma ×500. I, Reconstructed median transverse section of a stoma, ×500. All lettering gives the location of other figures.

and unmodified in size and orientation but sometimes are radially elongated from the stomatal aperture.

Comparison. Lacey (1962) has described a species of *Lepidodendron* from the Lower Carboniferous of North Wales as being nearest to *L. veltheimii*. His plate 16, fig. 16 shows the leaf cushions to be roughly 20×7 mm. with very little detail except a slight inflection of the upper and lower angles. The cuticle from the groove between the cushions has epidermal cells 100 μ×30 μ possessing thick (5–6 μ) anticlinal walls. These cells are larger and have thicker walls than those from the larger cushions of K 2411 so it is doubtful that the two specimens belong to the same species.

Lepidodendron feistmanteli Zalessky

Plate 33, fig. 3; Plate 34, fig. 5; text-fig. 6

1875 *Lepidodendron dichotomum* Sternberg; Feistmantel, p. 188, pl. 32, figs. 2, 4.
1904 *Lepidodendron Feistmanteli* Zalessky, p. 93, pl. 4, figs. 6, 10.
1913 *Lepidodendron Jaraczewski* Zeiller; Bureau, p. 113, pl. 40, figs. 1, 1*a*.
1944 *Lepidodendron Jaraczewski* Zeiller; Bell, p. 89, pl. 51, figs. 1, 2.

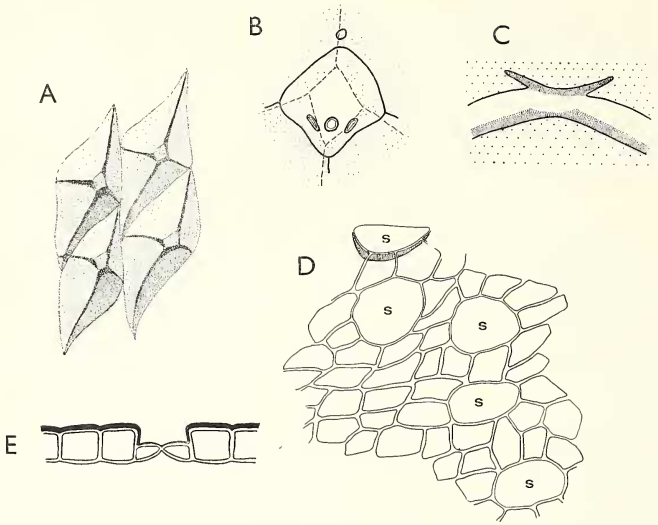
Material. GSM 77179, 77180 (part and counterpart); K 3255, 4874–6, 4946, 4993 from above the Fenton coal, Wooley and Dodworth collieries, near Barnsley, Yorkshire—communis zone, Westphalian A; K 3605 from the Bradford coal group, Bradford colliery, Lancashire—phillipsii zone, Westphalian C.

The largest piece of bark (GSM 77179) is 11 cm. broad and 33 cm. long and like all the other specimens shows no variation in cushion size or details. The leaf cushions are rhomboidal, strongly raised, and not continuous with the cushions above and below. The leaf scars are in the centre of the leaf cushions and raised above the general cushion area. The leaf scars have edges which slightly overlap the cushion and produce unequal partition of the compression when the rock is split. The carbonized compression of the scar is usually left in the counterpart producing what looks like a small unmarked scar on the elevated cushions of the other part of the specimen (text-fig. 6A). No vascular prints nor ligule pit apertures are visible on such specimens but they can be clearly seen if the compression is removed from the sunken impressions of the counterpart. The cushion surfaces are smooth but have very prominent keels above and below the leaf scars and also possess strong keel-like ridges running from the edges of the leaf scars to the edges of the cushions. No external parichnos are present.

Cuticle description. The epidermal cells on the leaf cushion surfaces are isodiametric and 15–20 μ across, but the cells on the cushion edges are slightly elongated towards the cushion centre. The anticlinal walls are straight, smooth, and 1–2 μ thick. The periclinal walls are flat and smooth. The stomata are 300–350 per mm.^{2} and are about 45–50 μ long and 15–20 μ broad. The guard cells are sunken in pits, 3–6 μ deep with very little or no overhang of the pit aperture. The ligule pit cuticles are about 0·8 mm. long with rectangular cells, 15–20 μ long and 15 μ broad, in longitudinal files.

Comparison. Fischer (1904) included *L. feistmanteli* in *L. dichotomum* Sternberg and Hirmer (1927) believed them to be related. They are, however, clearly distinct in both cushion and cuticle details. The leaf scars of *L. dichotomum* are not elevated and are relatively further up the leaf cushion. The epidermis of *L. feistmanteli* is roughly the

same over the whole cushion but in *L. dichotomum* it is different above and below the leaf scar. The epidermal cells and stomata are also larger in *L. feistmanteli.*



TEXT-FIG. 6. *Lepidodendron feistmanteli* Zalessky. GSM 77179. A, Leaf cushions, ×2. B, Reconstruction showing elevated leaf scar overlapping part of the leaf cushion, ×10. C, Reconstructed section through part and counterpart of a leaf cushion compression to show the raised leaf scar and the unequal splitting of the carbon. Coarse shading represents the rock matrix and the fine shading the carbonized compression. D, Leaf cushion cuticle, ×400; stomata—s; slide PF 2870. E, Reconstructed median transverse section through a stoma, ×400.

Bureau (1913) and Bell (1944) described what appear to be specimens of *L. feistmanteli* as *L. jaraczewski* Zeiller, However *L. jaraczewski* has relatively longer cushions and the leaf scars are not so raised, have no overlap over the cushion surface, and are

EXPLANATION OF PLATE 31

Figs. 1–3. *Lepidodendron aculeatum* Sternberg; illustrating variation in cushion ornamentation and the separation of cushions by lateral stem expansion; ×1. 1, WM, G 541 from Tamworth, Staffordshire. 2, BMNH 46685, from Ebbw Vale, Monmouthshire. 3, BMNH 1049, from Waldenburg, Silesia.

Fig. 4. *Lepidodendron serpentigerum* Koenig. GSM 2498 from above the Stranger Coal, Grange Colliery, Kilmarnock, Ayrshire; ×2.

Fig. 5. *Lepidodendron barnsleyense* sp. nov. Holotype, K 4131, from above the Barnsley Bed, Monkton Main Colliery, Yorkshire; ×2.

Figs. 6, 7. *Lepidodendron dichotomum* Sternberg. Unlocalized specimen in the Huddersfield Museum; ×2. 6, Portion of compressed bark. 7, Impressions of cushions in the shale.

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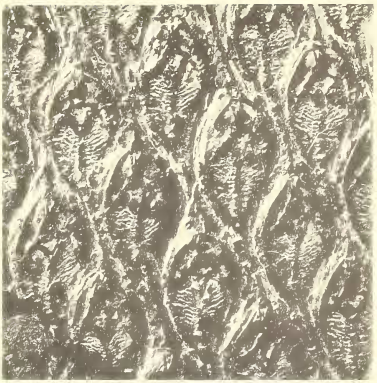

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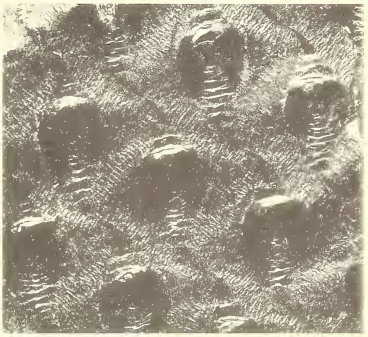

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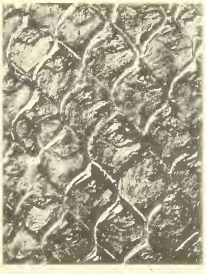

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THOMAS, *Lepidodendron*

situated further up the leaf cushions. *L. jaraczewski* also has less prominent keels and lateral lines running from leaf scar to cushion edge. These lateral lines are also not as straight as in *L. feistmanteli* but curve downwards to meet the cushion edge below the central broadest part of the leaf cushion.

Lepidodendron mannabachense Presl

Plate 30, figs. 3, 4; Plate 32; Plate 34, figs. 1, 2, 7, 8; text-figs. 7, 8

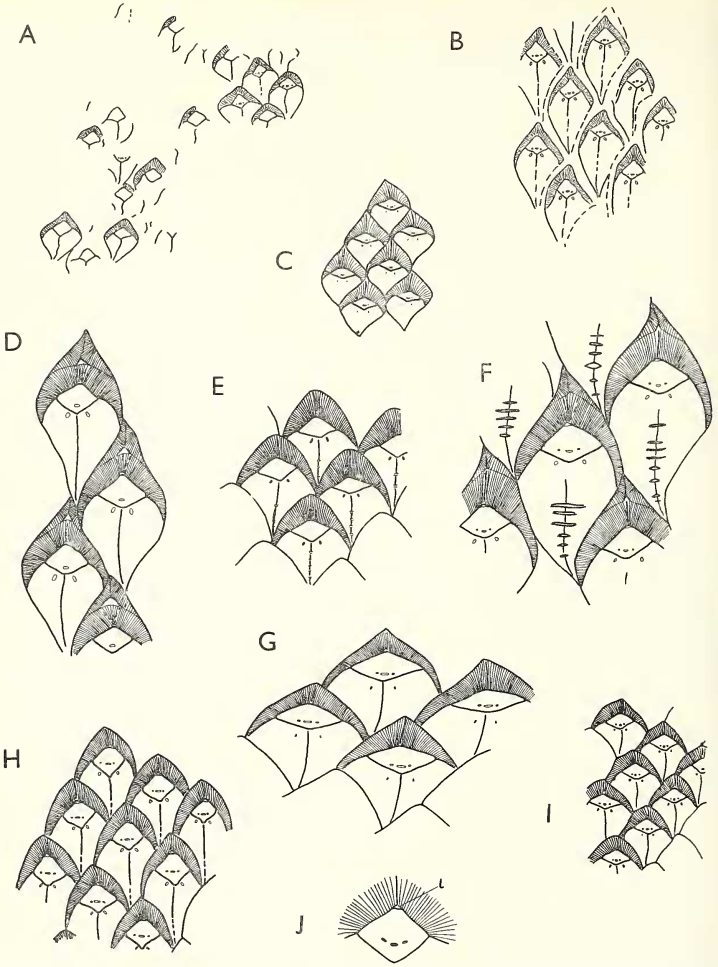
1838 *Lepidodendron mannabachense* Presl in Sternberg, p. 177, pl. 68, fig. 2.
1838 *Sagenaria obovatum* Presl in Sternberg, p. 178, pl. 68, fig. 6.
1886 *Lepidodendron obovatum* Sternberg; Zeiller, p. 442, pl. 66, figs. 1–8.
1904 *Lepidodendron obovatum* Sternberg; Renier, pl. 1, figs. *a*, *b*.
1947 *Lepidodendron obovatum* Sternberg; Němejc (in part), p. 51.
1959 *Lepidodendron obovatum* Sternberg; Remy, p. 100, fig. 77.
1964 *Lepidodendron obovatum* Sternberg; Crookall, p. 239, pl. 60, figs. 3, 4; text-fig. 776.
1966 *Lepidodendron obovatum* Sternberg; Thomas, fig. 3.

Material. Type specimen, CNM ČGH 329, from the Upper Carboniferous of Mannabach, Thüringen; CNM ČGH 335 (*S. obovatum* Presl in Sternberg 1838, pl. 68, fig. 6) from the Upper Carboniferous of Chomle; K 3365, from the Westphalian of Trawden Forest, near Colne, Lancashire; K 2469, Low main coal, Cramlington, Northumberland—Westphalian B; K 2473, Stanley Main coal, Thome's colliery, Wakefield, Yorkshire—Westphalian B; K 2474, Low Moor, near Bradford, Yorkshire—Westphalian A; SM M378, from the coal measures of Wakefield, Yorkshire; SM M1476, Queen's seam, Broomhill colliery, near Amble, Northumberland—Westphalian B; LM 265, 1958/1, Adam Head No. 1 pit, Desford colliery, Leicestershire, probably Westphalian A.

Both the specimens described by Presl are preserved as impressions with no compression remaining. Similar cuticles were, however, prepared from the other seven specimens. The cushion outlines are distinct but in some specimens their upper angles overlap the lower parts of the cushions above which is probably a compression feature produced during fossilization. The leaf scars are within the upper halves of the leaf cushion and have three foliar prints in their lower halves. The ligule pit apertures are adjacent to the upper angles of the leaf scars where they can be easily overlooked if cuticle preparations are not made. Traces of infrafoliar parichnos can be seen on some cushions of every specimen. The keels, which are always present, are smooth above the leaf scar but sometimes notched below it. The cushion surface below the leaf scar is smooth but above it there are many fine striations running from the scar to the cushion edge.

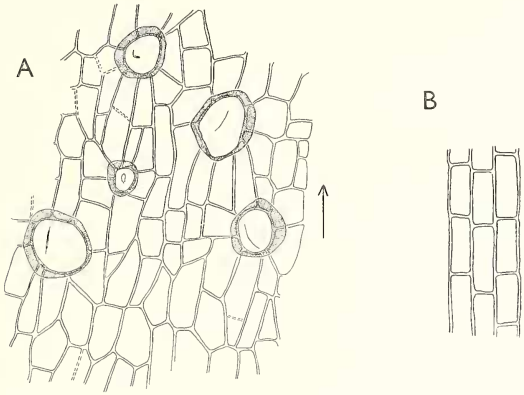
The range of leaf cushion size is a result of the different positions of the cushions on the parent plant, as the larger shoots always bore the larger cushions. The differences in cushion shape are small and can be regarded as variation within the species.

Cuticle description. The epidermal cells above and below the leaf scars are different. The cells above the scars are about 20–40 μ long and 10–15 μ broad and elongated from the scar to the cushion edge, while the cells from below the scars are isodiametric and 15–20 μ broad or sometimes elongated towards the scar and about 30–35 $\mu \times 15$ μ in size. Cells from the intercushion grooves are isodiametric and 15 μ broad, or elongated across the groove and about 15 $\mu \times 10$ μ. The anticlinal walls are straight, smooth and 1–2 μ thick. The periclinal walls are flat and faintly granular and occasionally have striations, less than 1 μ thick, across the cells. The stomata are about 200 per mm.^{2} and randomly



TEXT-FIG. 7. *Lepidodendron mannabachense* Presl. A, Type specimen, CNM ČGH 329. B, CNM ČGH 335. C, K 2469. D, SM M1476. E, K 2473. F, LM 256, 1958/1. G, SM, M378. H, K 3365. I, K 2474. All at ×2. J, Leaf scar with ligule pit (l), ×4. The shading lines indicate the areas covered by surface striations and their direction. They do not represent individual striations.

distributed on the cushion surface, but are absent in the intercushion grooves. Stomatal average size is about 25–30 $\mu \times 12\,\mu$ and the guard cells are sunken in pits about 6 μ deep. The subsidiary cells are unmodified and about eight per stoma. The ligule pit has rectangular cells 30 $\mu \times 10\,\mu$ along most of its length, but roughly square cells, 10 μ across, near its base.



TEXT-FIG. 8. Cushion cuticle of *Lepidodendron mannabachense* Presl. A, Leaf cushion cuticle from above the leaf scar, from K 3365, slide PF 2815. B, ligule pit cuticle, from K 2469, slide PF 2810. Both at $\times 400$.

Comparison. The distinction of *L. mannabachense* has already been dealt with above in the discussion of *L. aculeatum*. Cuticle study also supports the distinction of the two species as *L. mannabachense*, unlike *L. aculeatum*, has striations on the leaf cushions above the scars and a corresponding difference in epidermal structure above and below the scars.

Lepidodendron dichotomum Sternberg

Plate 31, figs. 6, 7; text-fig. 9

1820 *Lepidodendron dichotomum* Sternberg, pars, pl. 1, 2.
1838 *Lepidodendron dichotomum* Presl in Sternberg, p. 214, pl. 68, fig. 2; pl. A, fig. 16.
1838 *Lepidodendron Sternbergii* Brongniart, p. xiv, pl. 16, figs. 2, 3.
1875 *Lepidodendron dichotomum* Sternberg; Feistmantel, p. 188, pl. 32, figs. 1,3.
1934 *Lepidodendron dichotomum* Sternberg; Němejc, p. 1, pl. 1, figs. 2, 3; pl. 2, fig. 1.
1959 *Lepidodendron dichotomum* Sternberg; Remy, p. 100, text-fig. 78, *a*, *b*.
1964 *Lepidodendron dichotomum* Sternberg; Crookall, pars, p. 236.

Material. Type specimen, CMH ČGH 315, from the Upper Carboniferous of Svinná; K. 4876, from above the Parkgate coal, Dodworth, near Barnsley—Westphalian A; an unlocalized specimen in the Huddersfield Museum.

The specimens show shoots covered with diamond-shaped leaf cushions 2–5 mm. high and broad with angled corners. Some variation is shown in K 4876, where some cushions are slightly different being 2 mm. long and broad but with rounded lateral angles. Also certain shoots show different-shaped cushions in different parts; for example one has cushions 4 mm. long and 2 mm. broad in one part while elsewhere they are 2 mm. long and broad. The leaf scars are situated near the apices of the cushions and are roughly diamond-shaped and one and a half times as broad as high. Three foliar prints and two infrafoliar parichnos are present, though they are often indistinct. The ligule pit aperture is adjacent to the upper angle of the leaf scar. A very slightly raised keel can be seen, though it is usually more definite above than below the leaf scar. The cushion surface above the leaf scar shows many fine striations running from the leaf scar to the cushion edge, but the surface below the scar is smooth.

Cuticle description. The epidermal arrangement is different above and below the leaf scars. The cells above the scars are normally about 20–30 μ long and 15 μ broad and elongated from the scar to the cushion edge, although occasionally they are roughly isodiametric. These cells are often in short longitudinal rows running from the scar to the cushion edge. The cells below the leaf scars are normally roughly isodiametric and 10–15 μ broad but are sometimes slightly elongated towards the leaf scars. The intercushion grooves have isodiametric cells 15 μ across and cells 15 $\mu \times 10$ μ elongated across the groove. Anticlinal walls are straight, smooth, and 2 μ thick except above the leaf scar where they are often 4 μ thick. The periclinal walls are flat and faintly granular. Stomata are very frequent below the leaf scar, 450 per mm.^{2}, where they are randomly distributed and orientated. However, they are normally absent above the leaf scar except occasionally in the lower angles at the sides of the scar. Very few stomata are present in the intercushion grooves. Stomatal average size is about 40 $\mu \times 20$ μ and the guard cells are sunken in pits about 6 μ deep. The subsidiary cells are unmodified and are about ten per stoma. The ligule pit is about 0·6 mm. long and 0·13 mm. broad. The cells are mostly rectangular, 30 $\mu \times 10$ μ, and elongated along the pit, but are roughly square near its base.

Comparison. Much has been written about this species. Brongniart (1828*a*) followed by Presl in Sternberg (1838) restricted *L. dichotomum* to plates 1 and 2 of Sternberg's (1820) original description, excluding his plate 3. The species in this restricted sense has been widely recorded, although Jongmans (1929) and Crookall (1964) believed many of the specimens to be misinterpreted. Other authors have interpreted *L. dichotomum* in different ways including other combinations of specimens as synonyms, but as Němejc (1947) has given a useful summary no further review will be included here. However, some authors, including Němejc (1946 and 1947) and Chaloner (1967), have included *L. dichotomum* as a synonym of *L. obovatum* (= *L. mannabachense*) believing them to be the small and large shoots of one species. Although the smallest cushions included here as

EXPLANATION OF PLATE 32

Figs. 1–7. *Lepidodendron mannabachense* Presl, illustrating variation in cushion shape and size. All at ×2. 1, SM M1476. 2, LM 256, 1958/1. 3, K 3365. 4, K 2473. 5, K 2469. 6, K 2474. 7, K 378.

The localities are given on p. 157.

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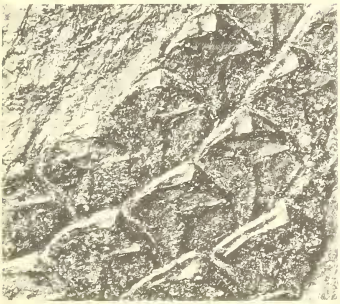

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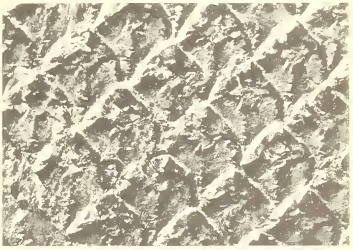

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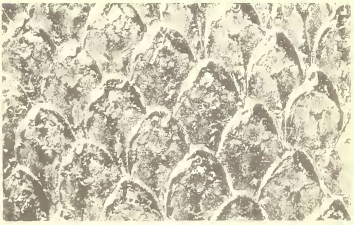

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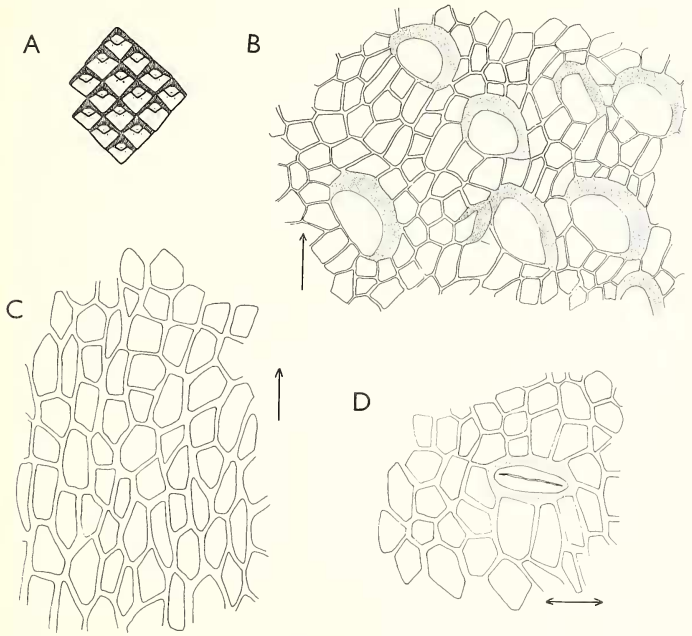
THOMAS, *Lepidodendron*

L. mannabachense are very similar to those of *L. dichotomum*, I favour, at least for the present, their continued separation. The leaf cushions of *L. dichotomum*, as interpreted here, are more diamond-shaped than those of *L. mannabachense* and the leaf scars are



TEXT-FIG. 9. *Lepidodendron dichotomum* Sternberg. A, Unnumbered specimen in the Huddersfield Museum. B, Leaf cushion cuticle from below leaf scar. C, Leaf cushion cuticle from above leaf scar. D, Cuticle from intercushion groove; arrows are parallel to groove. Magnifications: leaf cushions ×2; cuticles ×400

situated relatively higher on the cushions. The epidermal cells are larger in *L. mannabachense*, but more important is the difference in stomatal frequency between the two. In *L. dichotomum* stomata are almost completely absent above the leaf scar but are 450 per mm.^{2} below the scar, in contrast to *L. mannabachense* where they are roughly 200 per mm.^{2} over the whole cushion surface.

All the typical shoots of *L. dichotomum*, as described here, are narrow. However, it is reasonable to assume that the larger shoots of the species bore larger leaf cushions since leaf cushion and shoot sizes are generally supposed to be interrelated (Eggert 1961). Therefore, if *L. mannabachense* is not the larger form of *L. dichotomum* we should look

elsewhere for such shoots. Němejc (1934) described some specimens as *L. dichotomum* which have both larger leaf cushions and broader shoots than those described here. The leaf scars are diamond-shaped and are situated centrally on the cushions and not near their apices as in the more typical specimens described above. No cuticles could be prepared from Němejc's specimens and the rough surface of the compression prevented direct observation of individual epidermal cells. Striations were, however, visible above the leaf scar suggesting that the cells in this area were elongated while those below the scar were isodiametric, but this alone is not sufficiently characteristic for species distinction as several species are known to have such epidermal arrangements. These specimens cannot therefore be regarded as being definitely conspecific with *L. dichotomum*, although such a relationship is not impossible on the available epidermal evidence. Further work is clearly needed before the larger shoots of *L. dichotomum* are known with certainty.

Lepidodendron subdichotomum Sterzel pars

Text-fig. 10, E–H

1855 *Sagenaria dichotoma* Sternberg; Geinitz pars, p. 34, pl. 3, figs. 2–5, 9.
1901 *Lepidodendron subdichotomum* Sterzel pars, p. 106.
1903 *Lepidodendron dichotomum* Zeiller (?Sternberg); Arber, pp. 20, 32, pl. 1, figs. 1, 2.
1904 *Lepidodendron dichotomum* Sternberg; Zalessky pars, pp. 9, 83, pl. 3, figs. 5, 10, 10*a*, 11.
1914 *Lepidodendron dichotomum* Sternberg; Arber, pp. 402, 445, pl. 29, fig. 36.
1922 *Lepidodendron loricatum* Arber pars, p. 201, pl. 13, figs. 27–32.
1925 *Lepidodendron loricatum* Arber; Crookall, p. 170.
1929 *Lepidodendron loricatum* Arber; Crookall, p. 25, pl. 3, fig. *h*; pl. 20, fig. *h*.
1929 *Lepidodendron loricatum* Arber; Jongmans, p. 208.
1929 *Lepidodendron subdichotonum* Sterzel; Jongmans, p. 313.
1947 *Lepidodendron subdichotomum* Sterzel; Němejc pars, p. 57, pl. 1, fig. 7.
1964 *Lepidodendron loricatum* Arber pars; Crookall pars, p. 243, pl. 64, fig. 9; text-fig. 79.

Material. Syntype of *L. loricatum*, SM 2506, from the Sulphur Coals, Transition Coal Measures, Bayton Colliery, Wyre Forest, Worcestershire, Westphalian C; K. 6340, No. 3 Llantwit Seam, Cross Inn, Llantrisant, Glamorgan, Westphalian C.

The leaf cushions are close together but not continuous with those above and below. The leaf scars are about two-thirds the distance up the leaf cushions and are often arranged obliquely on the cushions. There is no keel above the leaf scar, only a faint keel below the scar and no lateral lines running from the scars to the cushion edges. Three foliar prints can be indistinctly seen about one-third the distance up the scars but there are now visible infrafoliar parichnos. The ligule pit apertures are adjacent to the upper

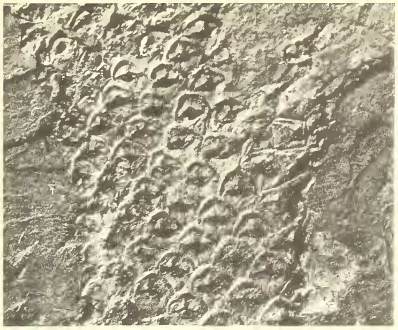
EXPLANATION OF PLATE 33

Fig. 1. *Lepidodendron peachii* Kidston. K 2466, from the Lower Main Seam, Newsham, Newcastle upon Tyne, ×2.

Fig. 2. *Lepidodendron arberi* sp. nov. Holotype, K 2488, from the Lower Main Coal, Cramlington, Northumberland, ×2.

Fig. 3. *Lepidodendron feistmanteli* Zalessky. GSM 77179, from the Fenton Coal, Wooley, Yorkshire, ×2.

Figs. 4–6. *Lepidodendron veltheimii* Sternberg. K 2411, from immediately beneath the Orchard Limestone, New Brawden Quarry, Giffnock, Renfrewshire. 4, Leaf cushions, ×2. 5 and 6, Leaf cushion cuticle, slide PF 2700; 5, Epidermal cells and stomata on and near the keel below the leaf scar, ×25; 6, Obliquely compressed stomata showing pit cuticles but no guard cells, ×400.



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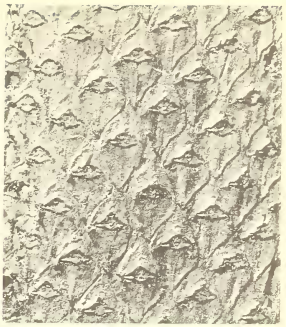

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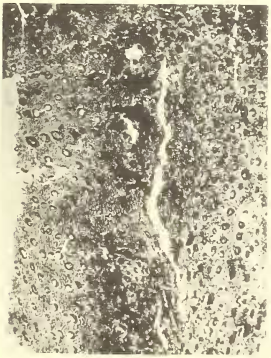

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angles of the leaf scars. The leaf cushion surfaces are smooth above and below the leaf scars.

Cuticle description. The epidermal arrangements are roughly the same above and below the leaf scars. The epidermal cells from the central area of the cushions are isodiametric and about 15–20 μ across. The cells from the edges of the cushions are elongated towards the leaf scars and are about 30 μ long and 10 μ broad. The anticlinal walls are straight, smooth and about 1 μ thick. The periclinal walls are flat and smooth. The stomata are about 200 per mm.^{2} and of average size 38 $\mu \times 26$ μ, with superficial guard cells. The ligule pits have rectangular cells, in longitudinal rows, which are 40 $\mu \times 10$ μ in size along most of the pit except near the base where they are roughly 10 μ square.

Comparison. Sterzel instituted *L. subdichotomum* for some specimens from Sachsen which had been previously identified by Geinitz (1855) as *Sagenaria dichotoma* Sternberg (pl. 3, figs. 1–12) and *Sagenaria rimosa* Sternberg (pl. 3, figs. 13–15). Arber (1922) also included the *S. dichotoma* of Geinitz as a synonym of his *Lepidodendron loricatum* making no reference to Sterzel, although if both authors were correct in their determinations, his species was merely a later synonym for *L. subdichotomum*. The major problem, as usual, is deciding how much variation occurs within the species and what specimens are conspecific. Sterzel had not included in synonymy all the figures of *S. dichotoma* and *S. rimosa* given by Geinitz, while Arber suggested that possibly only two figures of *S. dichotoma* of Geinitz were the same species as his *L. loricatum*. Crookall included only a part of the *S. dichotoma* of Geinitz (pl. 3, figs. 2–5, 9) and only the plate 13, figs. 27–32 of Arber in his synonymy for *L. loricatum*, but like Arber made no reference to Sterzel. Such an acceptance of partial conspecificity of Geinitz's and Arber's specimens seems the best solution, but Sterzel's work should not be excluded as it has priority even though it is accepted in a reduced form. *L. subdichotomum* is therefore the correct name for specimens of this form.

Those figures quoted for *L. loricatum* by Crookall are given in synonymy here but three of his additional specimens are excluded. His plate 61, fig. 1 is probably *L. mannabachense* as the specimen has faint striations on the cushion surfaces above the leaf scars; plate 64, fig. 6 is described here as *Lepidodendron barnsleyense* sp. nov.; and plate 64, figs. 7, 8 has relatively highly placed leaf scars and infrafoliar parichnos making it unacceptable as *L. loricatum*, though I do not suggest another name. Three of Arber's specimens are also excluded from the present synonymy. Two (pl. 13, figs. 33–5) are described here as *L. arberi* sp. nov. and one (pl. 13, figs. 36, 37) looks more like *L. fusiformis* Corda.

Crookall (1964, p. 242) believed that most of the specimens identified by Kidston as *L. obovatum* (= *L. mannabachense*) were really *L. loricatum* (= *L. subdichotomum*) and that the latter species was the more common in Great Britain. The confusion of these two species by Crookall, as illustrated above by his plate 61, fig. 1, probably accounts for this view which appears incorrect when they are interpreted with the extra evidence afforded by epidermal studies.

Lepidodendron arberi sp. nov.

Plate 33, fig. 2; text-fig. 10, A–D

1922 *Lepidodendron loricatum* Arber pars, p. 201, pl. 13, figs. 33–5.
1964 *Lepidodendron* sp. Crookall, p. 303, pl. 72, fig. 5.